

Microtus pinetorum. By Michael J. Smolen

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Microtus pinetorum (LeConte, 1830)

Woodland Vole or Pine Vole

Psammomys pinetorum LeConte, 1830:133. Type locality pine forests of Georgia, probably near Riceboro, Liberty Co. (see Bailey, 1900).

Arvicola scalopsoides Audubon and Bachman, 1841:97. Type locality Long Island, New York.

Arvicola apella LeConte, 1853:405. Type locality Pennsylvania. *Arvicola kennicottii* Baird, 1858:547. Type locality Illinois.

Pitymys parvulus Howell, 1916:83. Type locality Lynne, Marion Co., Florida (see Howell, 1934).

CONTEXT AND CONTENT. Order Rodentia, Family Cricetidae, Subfamily Microtinae, Genus *Microtus*, Subgenus *Pitymys*. The subgenus contains two Nearctic and 15 Palaearctic species (Corbet, 1978). The species *M. pinetorum* contains seven subspecies as follows:

M. p. auricularis Bailey, 1898:90. Type locality Washington, Adams Co., Mississippi.

M. p. carbonarius (Handley, 1952:152). Type locality Eubank, Pulaski Co., Kentucky.

M. p. parvulus (Howell, 1916:83), see above.

M. p. pinetorum (LeConte, 1830:133), see above.

M. p. nemoralis Bailey, 1898:89. Type from Stilwell, Adair Co., Oklahoma.

M. p. scalopsoides (Audubon and Bachman, 1841:97), see above (*apella* LeConte, *kennicottii* Baird are synonyms).

M. p. schmidtii (Jackson, 1941:201). Type locality Worden Township, Clark Co., Wisconsin.

DIAGNOSIS. The subgenus *Pitymys* differs from the subgenera *Herpetomys* and *Orthiomys* in possessing an m3 with three transverse loops and no closed triangles (Fig. 1). It also differs from the subgenera *Microtus* and *Chilotus* in that those subgenera have M3 with three closed triangles while *Pitymys* has but two closed triangles (Bailey, 1900).

The differences in external appearance are quite distinct between the subgenera *Pedomys* and *Pitymys*. *Pitymys* (Fig. 2) is adapted for a semi-fossorial life (as opposed to terrestrial), has a smooth, silky, chestnut-colored fur (as opposed to a long, coarse, hispid fur), reduced eyes and ears (as opposed to enlarged and conspicuous), and fore claws distinctly larger than the hind claws (as opposed to same sizes). Furthermore, *Pitymys* has four mammae (4 inguinal) whereas *Pedomys* has six (2 pectoral; 4 inguinal) (Coues and Allen, 1877).

The cranial characteristics of the subgenera *Pedomys* and *Pitymys* are identical in most instances. However, characters of the first lower molar can separate these species (Martin and Webb, 1974). The anterior enamel border of the fourth triangle slopes posteriorly from an anteroposterior midline of the tooth at an angle of 50° or less, and the apex of this triangle does not tilt anteriorly. *Microtus ochrogaster*, on the other hand, differs in that this anterior enamel border forms an angle of 60° or greater with the anteroposterior midline of the tooth, and the apex of this triangle usually tilts somewhat anteriorly. An additional character, though less reliable, involves the sixth re-entrant fold in the first lower molar (Martin and Webb, 1974). The re-entrant fold of *M. pinetorum* is usually deep and curves into the anterior trefoil, while this fold is usually shallow and does not curve into the trefoil in *M. ochrogaster*. Those *M. pinetorum* that do not exhibit this morphological difference can usually be identified using the previously mentioned characters.

Microtus pinetorum can also be distinguished from *M. (Pitymys) quasiator* on the basis of the morphology of the lower first molar. The anterior loop of pine voles has incipient sixth and seventh triangles and shallow eighth and ninth re-entrant angles. These features produce a well-developed capsular process with an open anterior loop. *M. quasiator*, on the other hand, has deep re-entrants and a closed anterior loop caused by deep inflection

of the sixth and seventh re-entrants. A reduced capsular process is evident (Martin and Webb, 1974).

GENERAL CHARACTERS. The body is cylindrical, slender, and modified for semi-fossorial life. Fur is soft and dense; ears, eyes, and tail are reduced; facial vibrissae are well developed; the mouth is small and the upper lips are closely appressed beneath the upper incisors. The feet have five plantar pads. Females bear two pairs of inguinal mammae (Miller, 1896; Bailey, 1900; Hall and Cockrum, 1953).

The skull (Fig. 3) has relatively small squamosal crests with widely separated supraorbital ridges in the vicinity of the inter-orbital region. The tympanic bullae are small, and the molars are narrow (Coues and Allen, 1877; Hall and Cockrum, 1953).

External measurements (in mm) for samples of *M. p. auricularis* (Lindsay, 1960), *M. p. carbonarius* (Handley, 1952), *M. p. pinetorum* (Golley, 1962), *M. p. scalopsoides* (Benton, 1955), and *M. p. schmidtii* (Schmidt, 1931), respectively, are as follows (sex or age class, mean, range, sample size): total length, male 117.8 (111 to 124) 5, female 122.9 (113 to 131) 13; adults 125 (118 to 139) 10; male 111 (81 to 134) 17, female 116 (111 to 125) 6; adults 121.0 (113 to 132) 25; adults 120 (102 to 132) 29; length of tail, male 21.2 (21 to 22) 5, female 21.3 (18 to 14) 13; adults 23 (19 to 26) 10; male 18 (13 to 26) 17, female 19 (12 to 29) 6; adults 21.3 (16 to 24.5) 25; adults 21 (18.5 to 25) 29; length of hind foot, male 17.2 (17 to 18) 5, female 17.8 (16 to 19) 13; adults—not recorded; male 16 (13 to 19) 17, female 16 (14 to 18) 6; adults 16.6 (14.5 to 18) 25; adults 17.7 (17.5 to 18) 29.

Average weights (in grams) of *M. p. pinetorum* are: male 20.4 (19.0 to 23.2) 32, female 22.2 (19.5 to 24.5) 28 (Gentry, 1968); and male 24.2 (14.5 to 28.6) 17, female 27.4 (23.1 to 30.8) 6 (Col-

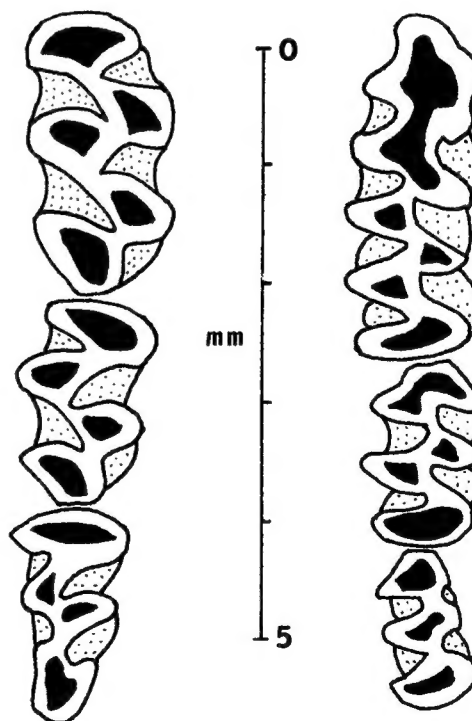


FIGURE 1. Occlusal views of right upper (A) and right lower (B) molar tooth rows. Anterior is at the top. The dentine is black, enamel is open, and cement is stippled. Based on CM 35667, from 4 mi NE McCrea, Cumberland Co., Pennsylvania.



FIGURE 2. Photograph of *Microtus pinetorum* from near Biglerville, Pennsylvania.

ley, 1962). Weights of *M. p. scalopsoides* are: adults 25.6 (22 to 37) 25 (Benton, 1955). A geographical cline in body size, increasing with latitude, is thought to occur in *M. pinetorum* (Arata, 1965; McNab, 1971).

Cranial measurements (in mm) of 10 *M. p. carbonarius* (Handley, 1952) are: greatest length of skull, 25.6 (25.1 to 26.6); zygomatic breadth, 15.5 (14.9 to 16.6); least interorbital width 4.4 (4.1 to 4.6); nasal length 7.8 (7.7 to 8.0); M1-M3 alveolar length 6.4 (6.2 to 6.7); mastoid breadth 13.0 (12.3 to 13.6); length of brain case, 13.3 (13.0 to 13.6).

DISTRIBUTION. *Microtus pinetorum* occurs throughout most of eastern United States and extreme southern Ontario, Canada (Fig. 4). The southern extent of its range forms near 30°N latitude, although a narrow lobe protrudes into northcentral Florida. The western edge of the distribution is less precise, especially in Texas. Patton (1963) hypothesized that climatic changes associated with glaciation in the Pleistocene shifted the natural arid environment to a more mesic grassland and allowed expansion of the range of *M. pinetorum* throughout the southwestern states and northern Mexico. The range dwindled, but persisted, in major parts of Texas through the middle 19th century (Semken, 1961, 1967). This greater range is borne out by the extensive fossil record in Texas (Lundelius, 1960; Patton, 1963; Semken, 1961, 1967) and northern Mexico (Hibbard, 1955). The current distribution of pine voles in Texas is unclear. Recent specimens have been collected on and about the Edwards Plateau, Kerr County (Bryant, 1941), but these are postulated to be relictual populations which are isolated from populations in eastern Texas (Dalquest et al., 1969).

FOSSIL RECORD. The similarities in dental morphology among species of microtines and the lack of sufficient analysis of fossils have hindered an accurate assessment of relationship among extinct and extant species. Positive identification of morphologically similar species, especially of *Microtus pinetorum* and *Microtus ochrogaster*, is extremely difficult, and frequently depends on "geographic probability" and "faunal assemblages" (Guilday et al., 1977). The distributions of extinct species are for the most part unknown, and therefore, cannot provide adequate information concerning phylogenies.

The origin of *Microtus pinetorum* is suspected to be either from *Microtus (Pitymys) hibbardi* (early Rancholabrean-Sangamonian, Martin and Webb, 1974) or from *M. (Pitymys) cumberlandensis* (Middle Irvingtonian, van der Meulen, 1978). Fossil records of *M. pinetorum* are limited to the Pleistocene. These sites are: Florida—Devil's Den, Levy Co. (Martin and Webb, 1974). Texas—Longhorn Cavern, Burnett Co. (Semken, 1961); Rattlesnake Cave, Kinney Co. (Semken, 1967); Friesenhahn Cave, Bexar Co. (Lundelius, 1960). Virginia—Natural Chimneys, Augusta Co. (Guilday, 1962); Clark's Cave, Bath Co. (Guilday et al., 1977). Pennsylvania—New Paris Sink-holes, Bedford Co. (Guilday and Bender, 1958; Guilday et al., 1964); Bootlegger Sink, York Co. (Guilday et al., 1966). Tennessee—Baker Bluff Cave, Sullivan Co. (Guilday et al., 1978). Mexico—Valley of Teguixquiac (Hibbard, 1955).

FORM. Fuzzy juvenile pelage is lost when three weeks old, and is replaced by a subadult pelage. Adult pelage appears short-

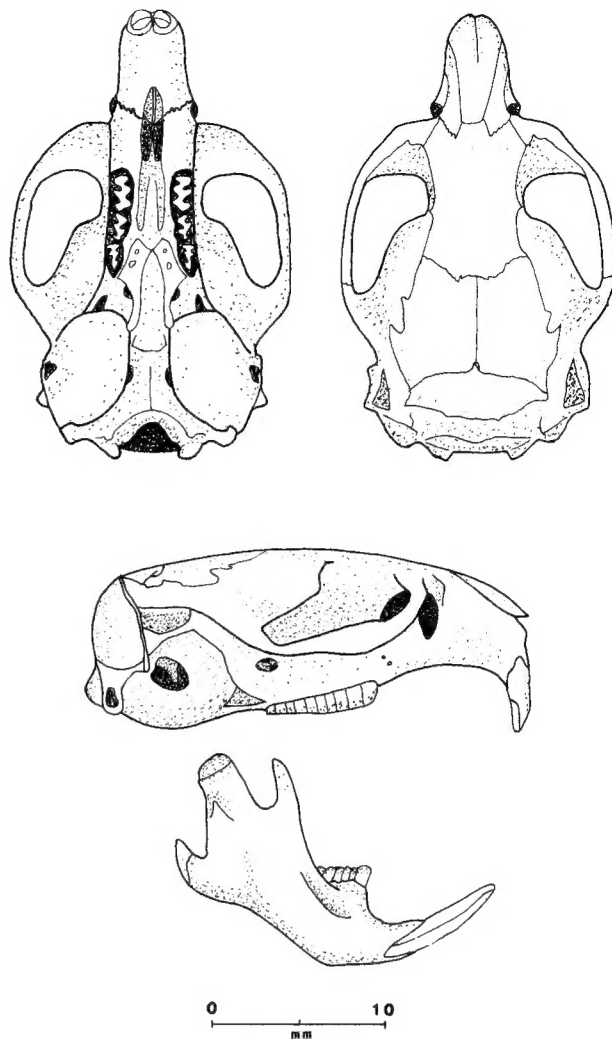


FIGURE 3. Ventral, dorsal, and lateral views of cranium, and lateral view of lower jaw of *Microtus pinetorum scalopsoides* from 4 mi NE McCrea, Cumberland Co., Pennsylvania (CM 35667).

ly afterward, beginning on the sides, near the forelimbs, and proceeding forward and upward over the shoulders and head. Simultaneously, hair replacement proceeds backward along the sides, then gradually backward along the back, ending on the rump (Benton, 1955; Hamilton, 1938). Molt on the ventral surface closely follows that on the sides. Adult pelage may be acquired in 7 to 10 weeks.

Molting occurs biannually. The darker pelage in winter is replaced during May or June by a light chestnut pelage dorsally. Winter molt begins in November and is completed in 3 weeks (Hamilton, 1938).

Color aberrations in pelage are not uncommon. Albinos were reported by Schantz (1960), and Paul (1964). Other specimens were described as rich orange-yellow with a light yellow ventral surface (Owen and Shackelford, 1942); and a variation in deposition of pigment produced voles which were light vinaceous-cinnamon with a white belly or all black (Handley, 1953).

The structure of the baculum was described by Anderson (1960), Burt (1960), Hamilton (1946), and Hooper and Hart (1962). Anderson (1960) described the bacula of *M. pinetorum* and *M. parvulus*, and stated that they differ only in size. The ossified stalk is broad; its greatest length is 2.5 to 2.7 mm (Anderson, 1960), which is about 1.7 times its greatest breadth and 4 times its greatest depth. The median process is also ossified and is about 20% of the length of the stalk. The lateral processes are cartilaginous.

The crater rim of the glans penis has no papillae (Fig. 5). The lateral bacular mounds are small in diameter, but are moderately long and unobscured by tissue folds. The urethral process

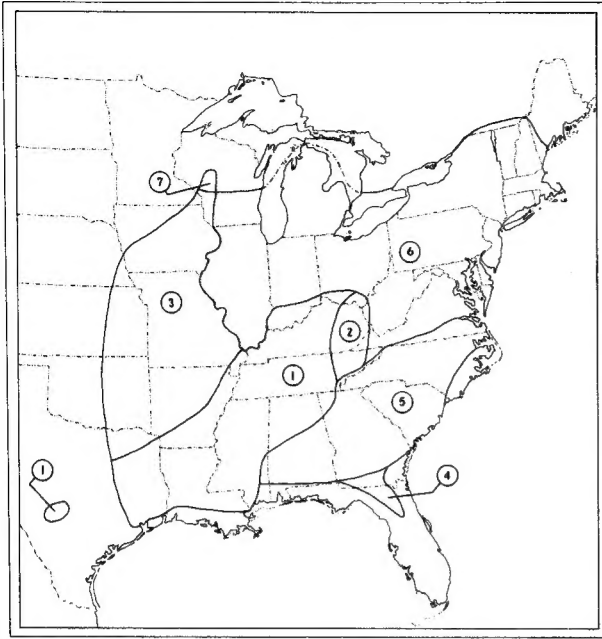


FIGURE 4. Geographic distribution of *Microtus pinetorum* and its subspecies: 1) *M. p. auricularis*, 2) *M. p. carbonarius*, 3) *M. p. nemoralis*, 4) *M. p. parvulus*, 5) *M. p. pinetorum*, 6) *M. p. scalopsoides*, 7) *M. p. schmidtii*. Modified from Hall and Cockrum (1953).

is a rectangular flap which is wider than long and serrate along the distal edge. The ventral shield is large. The baculum is 115% of the length of the glans. A more detailed description and discussion of the systematic implications of the structure of the glans of *M. pinetorum* are given by Hooper and Hart (1962).

Male accessory reproductive glands were fully described and their taxonomic relationships to other murid rodents were discussed by Arata (1963). These glands include a single pair of preputial glands, large and irregular vesicular glands, ampullary glands, and four pairs of prostate glands.

The dental formula of *M. pinetorum* is $i1/1, c0/0, p0/0, m3/3$, total 16. Coues and Allen (1877) provided a further description of the dentition. The m3 consists of three spherical to triangular shaped dentine islands in a single series on the tooth. The m2 has a posterior spherical triangle followed by an interior closed triangle, then an exterior closed triangle, then two angles which are generally confluent but sometimes separated by an enamel wall into two separate lateral closed triangles. The m1 has a posterior spherical triangle followed by an interior closed triangle; then an exterior closed triangle; then another internal closed triangle; then two lateral angles (one on each side) which are not separated and closed by a median enamel zigzag, but with their dentine areas confluent and running into the dentine island of the anterior trefoil; five internal and four external angles are produced in all. The M1 has an anterior spherical triangle, two interior and two exterior lateral closed triangles, with the last exterior being postero-lateral. M2 resembles the M1 except for the lack of one interior triangle. M3 has an anterior spherical triangle, followed by another like it reaching across the tooth, with the posterior margin varying in form.

The diastemal palate lacks a true anterior longitudinal ridge, though there is an exposure of mucous membrane in this area. The inflexi of the upper lip are well developed. Ventral inflexi of the lower lip are sometimes discernable. Woodland voles also possess large sebaceous glands, medium-sized mucous glands, but small sudoriferous glands. See Quay (1954, 1965) for a full description of these features and their similarities to other microtine rodents.

The palatine slits of *M. pinetorum* are blunt and regular in their posterior termination, with neither slit extending noticeably farther than the other or being noticeably attenuated (Nichols, 1937). These characters are sufficient to distinguish *M. pinetorum* from some other species of the genus *Microtus*.

FUNCTION. Sealander (1964) described some basic blood parameters for pine voles. Mean erythrocyte diameter was 6.4μ

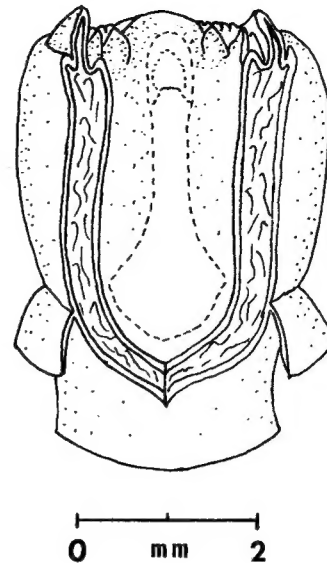


FIGURE 5. Ventral view of glans (incised midventrally) of *Microtus pinetorum*. Illustration modified from Hooper and Hart (1962).

(range 5.4 to 7.0, $n = 4$); the blood of pine voles has a high oxygen capacity for their body weight. Hemoglobin concentration (g/100 ml), hematocrit ratio (HCT %), and mean corpuscular hemoglobin concentrations for voles from two altitudes were as follows, respectively: adult males ($n = 3$ at 381 m) 17.1, 51.1, 33.6; adult female ($n = 1$ at 381 m) 18.8, 53.5, 34.4; adult male ($n = 1$ at 91.4 m) 17.0, 51.1, 33.3.

Water consumption of an 18.2 g male pine vole was recorded as 5.5 cc water/24 h in a laboratory study (Odum, 1944).

Estimates of the age of pine voles can be made by using a regression formula (Gourley and Jannett, 1975) of eye lens weight and known age. Confidence intervals in days for three animals known to be exactly 30-days old were $24 \leq A \leq 36$, $28 \leq A \leq 32$, $19 \leq A \leq 43$; and the intervals for three known 180-day old animals were $148 \leq A \leq 223$, $174 \leq A \leq 187$, and $124 \leq A \leq 282$, where A is the known age.

ONTOGENY AND REPRODUCTION. The breeding season extends from January through November for populations in the Northeast. Females in a population from New York were reproductively active by January, but were preceded by the testicular development of males which occurred in late December (Benton, 1955). Breeding began later (mid-February) in females in a population in Connecticut (Miller and Getz, 1969). Cessation of breeding in these populations occurred in October and mid-November, respectively, and was characterized by flaccid testes which were reduced in length (not exceeding 3 to 4 mm; Benton, 1955). A North Carolina population studied by Paul (1970), however, was reproductively active throughout the year, with a peak in July and a low from December to January. Populations from Oklahoma differed in that no reproduction occurred between May and August; most activity occurred in August, and October through April (Goertz, 1971; Glass, 1949).

Young first appear in late March (Hamilton, 1938) and continue to appear through July (Miller and Getz, 1969). Horsfall (1963) recorded an increase in percentage of pregnant females (New York) in April and peak pregnancies in August, while Cengel et al. (1978) observed a peak from July through September for a Virginia population.

Females showed no cyclic pattern of vaginal changes. The presence of a male is important in inducing estrus, as 50% of previously isolated females were in estrus on day 3 following pairing with males (Schadler and Butterstein, 1979). Post partum estrus was also observed (Kirkpatrick and Valentine, 1970); 87% of 132 litters were conceived within three days of parturition (Schadler and Butterstein, 1979). Glands located in the hip region of males may be responsible, in part, for stimulating females to receptivity (Benton, 1955). Females may bear from one to four litters per year (Goertz, 1971); in one study, 25 females had an average of 1.7 pregnancies (Gentry, 1968).

A vaginal plug forms and persists for about 3 days after copulation. It is a yellowish viscous mass occupying most of the vagina, but it is usually not visible externally (Benton, 1955). The vulva remains open for several days after mating, and may open again several days before parturition. Implantation probably occurs 5 to 7 days after copulation (Paul, 1970).

Following a gestation period of 20 (Golley, 1962) to 24 days (Kirkpatrick and Valentine, 1970), the young are born with a sprinkling of fuzzy hairs on the dorsum and well-developed mystacial bristles (Benton, 1955). Neonates weigh 1.9 to 3.2 g at birth (Goertz, 1971; Hamilton, 1938; Paul, 1970), can pull themselves about with short blunt claws on their forelimbs, and emit low squeaks and sucking noises when disturbed (Benton, 1955). They quickly attach to one of the four mammae of the mother, and are difficult to dislodge (Hamilton, 1938).

Full descriptions of the development of pine voles appeared in Hamilton (1938) and Paul (1970). Pups are born with eyes and ears closed, and have a total length of 39 to 48 mm (crown-rump length of 27 to 29 mm). Development is as follows: day 3—the dorsum is lead colored and the underparts are pink (TL = 43 to 54, Paul, 1970; external measurements 46-46-X = 3.7 g, Hamilton, 1938); day 5—the body is well covered with fine hair, with only the limbs and genital region pinkish (2.4 to 3.7 g; Paul, 1970); day 7—55-5-8-X = 5 g (Hamilton, 1938); day 8—ear pinnae unfold (Benton, 1955); day 9—smooth brown hair begins to appear dorsally, with gray fur ventrally—young crawl vigorously; eyes open between days 7 and 9 (TL = 53 to 69 mm; 3.1 to 6.4 g; Paul, 1970); day 12—they are very active and able to maintain balance well; ears open between days 11 and 12 (74-9-12-X = 7.0 g, Hamilton, 1938; TL = 58 to 81, 4.4 to 7.8 g, Paul, 1970); day 16—few still nursing, most begin to eat solid food (10-11 g; Hamilton, 1938). Lactation averages 20 days, and weaning occurs between days 17 and 21 (Geyer and Rogers, 1979; Hamilton, 1938; Paul, 1970).

At three weeks of age the voles have a total length of 69 to 98 mm and weigh 7.5 to 9.6 g. By week 5 they range from 80 to 105 mm and 12.4 to 17.1 g (Paul, 1970). Paul (1970) observed initiation of sperm production in juveniles 100 mm in total length, and fully matured sperm in individuals 117 mm in total length. The testes were 4 mm in length. Schadler and Butterstein (1979) observed sperm in the epididymis by 6 to 8 weeks.

Litter sizes (followed by the range and sample size) are: 2.0, 1 to 4, n = 149 (Horsfall, 1963); 2.0, 1 to 3, n = ? (Gentry, 1968); 2.2, 1 to 5, n = 138 (Paul, 1970); 2.6, ?, n = 19 (Goertz, 1971); 2.8, 2 to 4, n = 14 (Hamilton, 1938); and 3.1, 1 to 6, n = 150 (Schadler and Butterstein, 1979). The variation in litter sizes is thought to be affected by light intensity (Geyer and Rogers, 1979), differences in types and nutritive value of forage (Cengel et al., 1978), and size of pregnant female (Paul, 1970). Because females have but four mammae and the young attach firmly (Hamilton, 1938), large litters are unsuccessful. Schadler and Butterstein (1979) observed that only 40% of the litters of five pups survived to weaning, whereas no females with six pups successfully reared all of them.

Females matured from weeks 10 to 12. First conception occurred at day 77, though the average was day 105 (Schadler and Butterstein, 1979). Paul (1970) observed that females matured earlier than males.

Little is known concerning differences in survival rates between sexes or among age classes. Gentry (1968) observed no difference in survival between age groups. Average survival from one year to the next was 58% for adults and 57% for juveniles and young adults. Miller and Getz (1969) found an average survival of 2.6 months for voles in a high density upland population.

ECOLOGY. Populations of *Microtus pinetorum* occur in a wide variety of habitats throughout their range, varying from subclimax beech-maple forests with closed canopies and varying depths of leaf litter (Miller, 1964) to grassy fields with many bushes, patches of brambles, and mats of honeysuckle (Layne, 1958). Well drained soil with a thick ground cover of either litter or vegetation are common parameters in most habitat descriptions (Connor, 1953; Helme, 1902; Johnson, 1935; Miller and Getz, 1969; Paul, 1970; Quick and Butler, 1885; Rowley, 1902). Floral assemblages consisting of beech (*Fagus* sp.), red maple (*Acer rubrum*), red oak (*Quercus rubra*), black oak (*Q. velutina*), and white oak (*Q. alba*) were reported for pine voles collected in Vermont (Miller, 1964) and Connecticut (Miller and Getz, 1969). Pine voles have been reported in the following floral assemblages in the southern portions of their range: bermuda grass (*Cynodon dactylon*) and johnson grass (*Sorghum halepense*) in Louisiana (Crain and Packard, 1966); bluegrass (*Poa* sp.), brome grass

(*Bromus* sp.), and dewberry (*Rubus* sp.) in Arkansas (Black, 1936; Brown, 1964); buffalo grass (*Bulbils dactyloides*), spanish oak (*Q. falcata*), redbud (*Cervis reniformis*), and sumac (*Rhus lanceolata*) in Texas (Bryant, 1941); rosemary shrubs (*Andromeda* sp.), sand pine (*Pinus clausa*), and turkey oak (*Q. laevis*) in Florida (Neill and Boyles, 1955). Orchards provide ideal habitat in North Carolina because of the presence of dense ground cover and because grass and forb growth is enhanced by frequent mowing and fertilization (Paul, 1970). The floral assemblage in the northern Midwestern portion of the range consists of maple (*Acer* spp.), elm (*Ulmus* spp.), yellow birch (*Betula alleghaniensis*), basswood (*Tilia* spp.), ferns in Wisconsin (Schmidt, 1927); grasses and honeysuckle (*Lonicera* spp.) in Illinois (Layne, 1958); oak (*Quercus* spp.), and hickory (*Carya* spp.) in Michigan (Burt, 1940). Standing water is not a requirement for pine voles since they can subsist on dietary water contained in succulent vegetation (Benton, 1955).

Most studies of diet have been limited to the northern and eastern portion of the range. In New York and Pennsylvania, the diet of pine voles consisted of grass roots and stems in summer, followed by fruit and seeds in autumn, and bark and roots in winter (Benton, 1955). Food included poke berries and wild onions (Gifford and Whitebread, 1951), tuberous rootstocks of wild morning glory (*Convolvulus sepium*), roots of quack grass (*Agropyron repens*), broad-leaved dock (*Rumex obtusifolius*), stems of barnyard grass (*Echinochloa crusgalli*), witch grass (*Panicum* sp.), and leaves of *Ranunculus* sp. (Hamilton, 1938).

Forbes and grasses were also the main portion of the diet throughout the year in populations in Virginia (Cengel et al., 1978). Roots were not eaten in May through July, but were eaten beginning in September, and constituted 7 to 15% of the diet from January through March (Cengel et al., 1978).

In Tennessee and North Carolina, the fungus *Endogone*, fruit, and unidentified vegetation and seeds made up the diet (Linzey and Linzey, 1973); pine voles living in orchards ate mostly vegetation (99.5% volume), while those in deciduous forests fed on vegetation (66.6%) and seeds (32.4%).

In Indiana the diet comprised sprouts of white clover (*Trifolium repens*), fruit of red haw (*Crataegus coccinea*), and the tuberous roots of wild violets (*Viola cucullata*) (Quick and Butler, 1885). Other food sources are the roots of squirrel corn (*Dicentra canadensis*) (Saunders, 1932), Dutchman's breeches (*Dicentra cucullaria*) (Schmidt, 1931), peanuts, and grama grass (*Tripsacum dactyloides*) and its seeds (Audubon and Bachman, 1851), bark from briars, hickory nuts, hazel nuts, acorns from bur oak (*Quercus macrocarpa*) and white oak (*Q. alba*) (Kennicott, 1857), and lily bulbs (Odum, 1949).

Pine vole densities are usually greater in orchards than in natural hardwood forests (Hamilton, 1938), and may vary from 0 to 14.6 voles/ha, though as many as 80 to 90 voles were snapp-trapped from one area (Paul, 1970). A Pennsylvania population had peak densities in March and November and a low in August (Fisher and Anthony, 1976). Summer declines are possibly due to drying of the soil and humus (Paul, 1970). A population from Kansas, however, was unimodal with the peak density limited to March through May (Fitch, 1954). These shifts in density may be due primarily to changes in reproductive output; Paul (1970) observed that the numbers of adults remained constant through the year while juveniles fluctuated between 10 to 45% of the population. Females were more abundant in populations studied by Goertz (1971) and Miller and Getz (1969), which had sex ratios of 1:1.20 and 1:1.15, respectively. A population in New York consisted of 54.3% males (Gourley and Richmond, 1972).

Microtus pinetorum has a long history of economic conflict with man. These voles damage crops of sweet and white potatoes, peanuts, nursery stock, lily bulbs, planted seeds (Eadie, 1954; Odum, 1949), and especially orchard trees (Anthony and Fisher, 1977; Eadie, 1954; Hamilton, 1938). Horsfall (1963) hypothesized that a decrease in availability of herbaceous food, which is aggravated by a steadily increasing density of voles and a seasonal decrease in herbaceous productivity (Cengel et al., 1978), directs a shift in food preferences to include the roots and bark of orchard trees. Complete girdling of apple trees six inches or less in diameter is common (Hamilton, 1938), and the resulting damage is usually not suspected until the tree is past recovery (Eadie, 1954; Hamilton, 1938). On large trees, a steady attack reduces both health and productivity, and in extreme cases may cause death (Anthony and Fisher, 1977; Eadie, 1954). In West Virginia, more than 1000 trees, 18 years old, were killed in a single orchard (Eadie, 1954).

Control of pine voles in orchards is accomplished primarily by use of poisons and Trail Builder Machines (Ladd, 1972). Zinc

Phosphide (Zn_3P_2) is a highly toxic compound commonly applied to grains and apples, which provides reasonably effective control (Ladd, 1972). Endrin (1, 2, 3, 4, 10, 10-hexachloro-6,7-epoxy-1,4,4a,5,6,7,8,8a-octahydro-1,4-endo-endo-5,8-dimethanonaphthalene), applied as a ground spray, has also been demonstrated to have a controlling effect (Horsfall, 1972), but may have limited future use because pine voles with a history of treatment exhibited a 12-fold greater tolerance to endrin in a study by Webb and Horsfall (1967). A niacin antimetabolite [1-(3-pyridylmethyl)-3-(4-nitrophenyl)urea] (trade name RH 787; Byers, 1976), Chlorophacinone (Horsfall, 1972), and DMCT (Stehn et al., 1980) are currently being studied as other effective poisons and anticoagulants. A magnetic device ("Nature Shield") has been shown to be ineffective in pine vole control (Byers, 1979).

A major problem involved in control by poisoning is effective application. Because these voles are primarily semi-fossorial, broadcast surface applications are effective only if the bait is deposited in the runway system, and is therefore limited to control in small orchards. A specially designed bait-plugging machine has been used to place poison bait in the ground in rows, but the Trail Building Machine is effective only if these rows cross the burrow system of the voles. Endrin, RH 787, and Chlorophacinone are spray compounds that coat ground vegetation and kill upon ingestion.

Throughout its range, *M. pinetorum* commonly occurs together with *Parascalops breweri*, *Sorex fumeus*, *Napaeozapus insignis*, *Clethrionomys gapperi*, *Sorex cinereus*, *Peromyscus leucopus*, *Peromyscus maniculatus*, *Blarina brevicauda*, *Microtus pennsylvanicus*, or *Zapus hudsonius* (Benton, 1955), especially in the Northeast. *M. ochrogaster* is a common associate in the western portion of the range. *Parascalops breweri* is an especially close associate, and pine voles are frequently found sharing both active and non-active mole burrow systems (Eadie, 1939; Miller, 1964; Osgood, 1936). Extent of interactions with *M. pennsylvanicus* populations are not clear, because pine voles have been observed both to increase in density following a "crash" of meadow voles (Hamilton, 1938), and to coincide with a "cycle" in which both "crashed" simultaneously (Linduska, 1942).

Endo- and ectoparasites have both been recorded in *M. pinetorum*. Endoparasites include: acarina—*Atricholaelaps glasgowi* (Judd, 1950); helminths—*Catenotaenia pusilla* (Chandler and Melvin, 1951; Whitaker and Adalis, 1971); acanthocephalans—*Monofiliformis clarki* (Benton, 1955); nematodes—*Trichurus* sp. (Benton, 1955), *Oxyuris* sp. (Erickson, 1938); Protozoa—*Sarcocystis* sp. (Cosgrove and O'Farrell, 1965); cestodes—*Cladotaenia* sp. (Whitaker and Adalis, 1971), *Taenia* sp. (Erickson, 1938; Whitaker and Adalis, 1971), and tapeworm larvae (Benton, 1955). Ectoparasites include: mites—*Laelaps microti* (Hamilton, 1938), *Laelaps alaskensis*, *Haemolaelaps glasgowi*, *Myocoptes* sp., *Dermacarus* sp., and *Pygmephorus* sp. (Benton, 1955); louse—*Hoplopleura acanthopus* (Benton, 1955); *Hoplopleura* sp. (Hamilton, 1938); fleas—*Ceratophyllus* sp. (Hamilton, 1938), *Ctenophthalmus pseudagyntes* (Jameson, 1943; Benton, 1955), and *Doratomyia blarinae*.

Benton (1955) recorded the mites *Glycyphagus domesticus* and *Garmania bulbicola* in nest material; they may act as either commensals or parasites, or both.

In analysis of 50 pine vole stomachs, 38% had lesions, 10% had gastric squamous papilloma or epithelial hyperplasia, 16% had gastric submucosal edema, 6% had focal calcification of gastric muscle, and 14% had acute or chronic gastritis (Cosgrove and O'Farrell, 1965). Hamilton (1938) described a skin disease which causes great patches of fur and epidermis to slough off, leaving large glabrous patches on the head, shoulders, and flanks. A slight pustular excrescence forms, and is accompanied by redness and a general eczematous condition, which in several weeks forms a dry crust over the eyes. This condition causes blindness, which is accompanied by general weakness in the hind limbs and which ultimately results in complete paralysis and death.

The primary predators of *M. pinetorum* are species of Strigiformes and Falconiformes. Latham (1950), Parmalee (1954), and Rageot (1957) listed the following species: barn owl (*Tyto alba*), long-eared owl (*Asio otus*), screech owl (*Otus asio*), short-eared owl (*Asio flammeus*), great-horned owl (*Bubo virginianus*), barred owl (*Strix varia*), red-tailed hawk (*Buteo lineatus*), broad-winged hawk (*Buteo platypterus*), and marsh hawk (*Circus cyaneus*). Other predators are the pilot black snake (*Elaphe obsoleta*) (Barbour, 1951), red fox (*Vulpes fulva*), gray fox (*Urocyon cinereoargenteus*), and opossum (*Didelphis marsupialis*) (Latham, 1950).

BEHAVIOR. Pine voles are semi-fossorial and spend most of their time in sub-surface burrows and surface runways which

they construct. Digging behavior, described by Hamilton (1938) and Benton (1955), involves a shovelling motion with the head and neck, which loosens dirt. Incisors and forefeet may also be employed to further loosen soil (Hamilton, 1938). Loosened dirt is scratched out, pushed backwards using a backward and side-ward motion with the forefeet, and lastly, the hindfeet sweep the dirt further back. When the burrow has proceeded about 31 cm or so, the pine vole turns and pushes the accumulated debris out of the tunnel with its head (Benton, 1955). The exhumed soil is deposited under the leaf layer, forming piles 10 cm or more in diameter and 5.0 to 7.6 cm high (Schmidt, 1931).

Most burrowing activity occurs within 5 to 10 cm of the surface (Benton, 1955; Fitch, 1958; Hamilton, 1938; Schmidt, 1931) although some burrows may extend 15 (Raynor, 1960), 20 to 25 (Schmidt, 1931), or 31 cm (Benton, 1955; Hamilton, 1938); the length may depend on the depth of loam (Schmidt, 1931). Burrows are approximately 30 to 35 mm in diameter (Schmidt, 1931), and may incorporate old mole runways (Eadie, 1939; Fitch, 1958). In areas with a thick leaf and humus layer, surface runways may be constructed; they serve to connect entrances to subsurface burrow systems (Schmidt, 1931).

Nests are constructed in the burrow system and, though usually globular (Elston, 1937; Hamilton, 1938; Raynor, 1960), they can be saucer-shaped if constructed beneath a fallen log (Neill and Boyles, 1955). Three to four exits lead away from the nest (Benton, 1955; Elston, 1937; Hamilton, 1938). Raynor (1960) described a simple nest, 15 to 18 cm in diameter, constructed from dry grasses, leaf fragments, and a few entire privet leaves. Other simple grass and grass rootlet nests were described by Neill and Boyles (1955) and Quick and Butler (1885). A more complex design consisted of a 25 cm diameter outer shell of dead oak (*Quercus* sp.) and maple (*Acer* sp.) leaves, and an inner chamber consisting of fine grasses (Elston, 1937).

Territoriality is lacking, and a single burrow system and nest may accommodate social groups containing numerous adults of both sexes and their young (Fitch, 1958). Raynor (1960) described a nest containing an adult female (lactating and with 2 embryos of 6 mm) sharing a nest with three litters (3 male, 1 female, 18 to 20 days of age; 3 young 10 to 12 days; and 3 young 8 to 9 days).

Home range is limited to the burrow system (Fitch, 1958), and is spatially oriented both horizontally and vertically (Benton, 1955). Home range estimates based upon live-trap data were described by Burt (1940) and Fitch (1958).

There appears to be no difference in vagility between sexes (Burt, 1940). Movements of 60 m have been observed between trap intervals; however, these individuals returned to their old areas soon afterwards (Fitch, 1958). Homing behavior has also been observed (Benton, 1955).

Pine voles seem to be active throughout the day, with peaks of activity described as being diurnal (Hahn, 1908; Paul, 1970) or consistent throughout both light and dark portions of the day (Benton, 1955). Seasonal depressions in activity have been observed in the daylight hours (Gentry, 1968; Horsfall, 1963), and may be associated with increased summer air and soil temperatures (Paul, 1970).

Females are aggressors in mating behavior and they appear to be stimulated by pheromones released from glands situated on the hips of males (Benton, 1955). Copulation lasts only a few seconds (Benton, 1955; Dewsbury, 1976).

Vocalizations have been described as harsh chattering (Benton, 1955; Neill and Boyles, 1955), and can vary from a single or double note to 4 or 5 notes in rapid succession. Vocalization appears to be used as an alarm (Benton, 1955) or when fighting (Benton, 1955; Neill and Boyles, 1955).

GENETICS. The karyotypes of 18 pine voles from seven localities in Tennessee and Arkansas were described by Beck and Mahan (1978). All were identical, having a diploid number and fundamental number of 62. The autosomes are all acrocentric with the exception of one pair of small metacentric chromosomes. The X-chromosome is submetacentric and large; the Y-chromosome is a small acrocentric.

REMARKS. This account treats *Pitymys* as a subgenus of *Microtus*. There is, however, much confusion about the generic relationship of these voles. Some have elevated the subgenus *Pitymys* to the generic level, based primarily on differences in pelage, ecology, or dental morphology (van der Meulen, 1978). Others maintained inclusion within *Microtus* because of the similarities in cranial morphology (Hall and Cockrum, 1953), dental morphology (Dalquest et al., 1969), and glans (Hooper and Hart, 1962). This debate has persisted in the literature since 1896 (Miller), and has not yet been resolved.

Microtus—Greek *mikros* (small, little) and *-otus* (ear); *pinetorum*—Latin *pinetum* (a pine woods) and *-orium* (belonging to a place of). Common names include: pine vole, pine mouse, mole mouse, potato mouse, mole pine mouse, bluegrass pine mouse, and woodland pine mouse.

A bibliography of the recent literature of pine voles was compiled by Hiassen et al. (1978).

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